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A NEW SPECIES OF *CASTILLEJA* (SCROPHULARIACEAE) FROM SOUTHCENTRAL TEXAS WITH COMMENTS ON OTHER TEXAS TAXA

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ABSTRACT

Castilleja genevievana *sp. nov.* is described from Crockett, Pecos, Upton, and Val Verde cos., Texas, and one closely adjacent locality in Coahuila, México. It is most closely related to *C. integra* and *C. purpurea* var. *citrina* but is allopatric with both and morphologically distinctive in its entire leaves, unbranched trichomes, and yellow floral bracts and calyces. *Castilleja wootonii* (the type from southeastern New Mexico) is the correct name for the species in Jeff Davis Co., Texas, previously known as *C. ciliata* and assumed to be a narrow endemic. *Castilleja elongata*, which has been recognized primarily from Brewster Co., Texas, and a proposed but yet unpublished species endemic to Jeff Davis Co. are interpreted as merely intergrading elements of the widespread and variable *C. integra*. *Castilleja latebracteata* (the type from Texas) is a synonym of *Castilleja rigida* (the type from Chihuahua), a species primarily distributed in northern México. *Castilleja tortifolia* (the type from Texas) is conspecific with the earlier named *C. mexicana*, also most abundant in northern México.

KEY WORDS: *Castilleja*, Scrophulariaceae, Texas, México

I. A new species from southcentral Texas

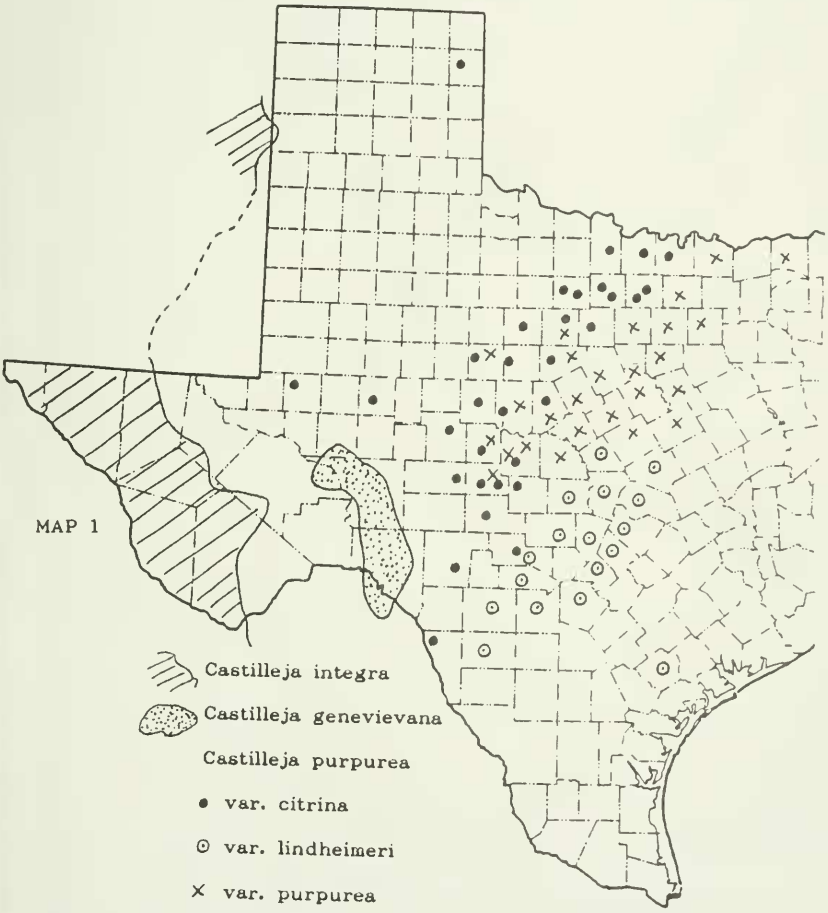
In his taxonomic treatment of Texas *Castilleja*, Holmgren (1970) noted that a population of *C. integra* A. Gray in Crockett Co. represented a geographically outlying segment different from the rest of the species in its "yellowish inflorescences and shorter floral measurements" and might prove to be distinct. These yellow flowered plants occur on the western edge of the Edward's Plateau of southcentral Texas, where they are now known from Pecos, Upton, and Val Verde cos., as well as Crockett Co. and from one closely adjacent

locality in Coahuila, México (Map 1). They are completely geographically separated from *C. integra*, which in Texas is restricted to the trans-Pecos area and which produces red bracts and calyces as well as a different vestiture. The Crockett Co. plants are more similar in vestiture, bracteal morphology, and coloration to *C. purpurea* (Nutt.) G. Don var. *citrina* (Penn.) Shinners, which occurs primarily from central Texas northward and which has a different leaf and floral morphology. Specimens of these geographically intermediate plants have most often been identified with caveats as *C. integra* or as *C. purpurea* var. *citrina*, and indeed they appear to be most closely related to both of these latter two taxa. As discussed below, however, they are distinct from both and may be justifiably regarded as a separate species.

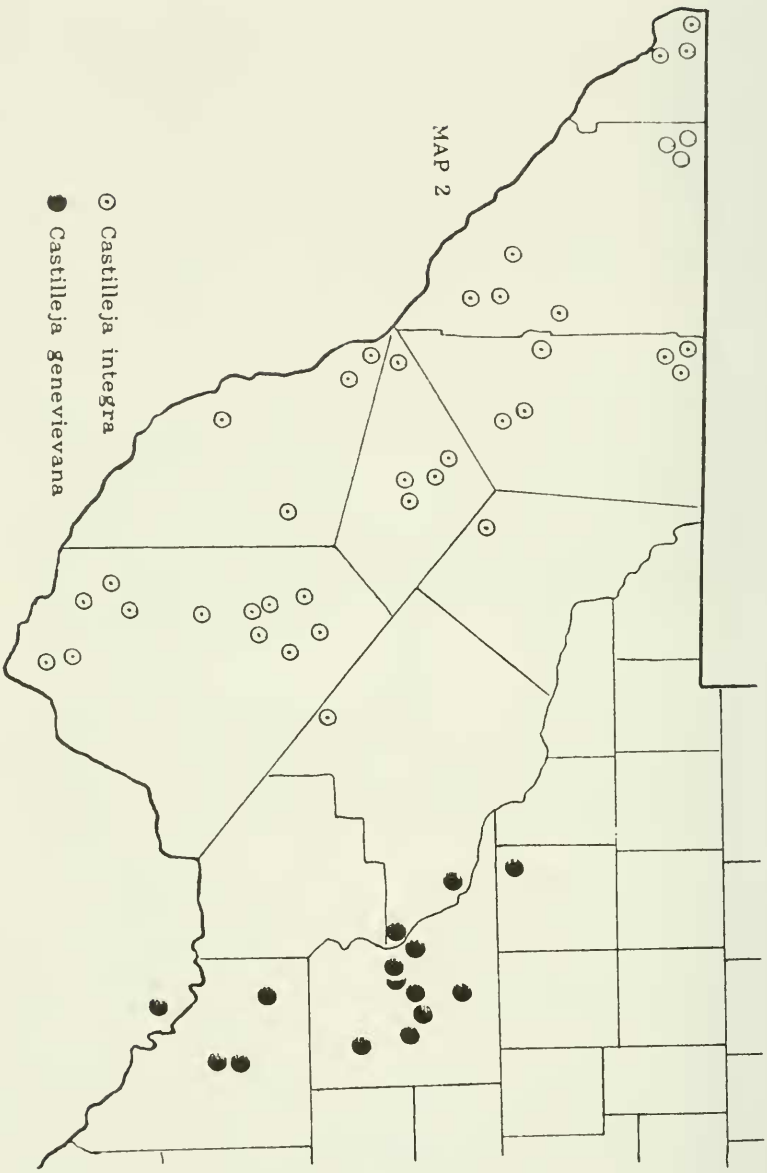
Castilleja genevievana Nesom, *sp. nov.* TYPE: UNITED STATES. Texas: Crockett Co., Hwy 290, 1.5 mi WSW of jct with Hwy I-10, ca. 24 mi W of Ozona (jct of I-10 and Hwy 163); area of steep limestone hills with dominant junipers, 2500 ft elevation, ca. 80 plants in an area of ca. 250 square yards, road bank and among scattered shrubs to fenceline; 5 April 1992, *Guy & Genevieve Nesom 03* with Julia Nesom (HOLOTYPE: TEX!; Isotypes: ANSM!,BRIT!,COLO!,GH!,MO!,NMC!,NY!,PH!,SRSC!,SWT!, TAES!,UC!,UNM!,UTEP!).

Castillejae integrae A. Gray ac *C. purpureae* (Nutt.) G. Don var. *citrinae* (Penn.) Shinners similis sed ab uterque proprius habitatione et distributione geographica, vestimento trichomatum non ramosis, foliis plerumque integris, bracteis ac calycibus flavis, bracteorum lobis anguste lanceolatis, et corollarum lobis infernis comparate brevioribus.

Plants perennial from strongly developed woody roots. Stems branched at base, the branches erect or ascending, 15-45 cm tall, loosely lanate with a moderate to dense investment of multicellular, unbranched, flattened, and vitreous hairs 0.5-2.0 mm long, these most commonly becoming somewhat tangled, often deflexed or retrorsely oriented, glandular hairs absent. Leaves linear-lanceolate, strongly 3 veined, 3-7 cm long, 4-8 mm wide, entire or the uppermost (rarely from midstem upwards) with a pair of linear or filiform lobes originating on the distal third of the blade, the adaxial surfaces moderately to densely invested with short, stiffly erect hairs, the abaxial surfaces glabrous or very sparsely hairy, margins densely long ciliate or at least with hairs distinctly longer than on the surfaces. Mature inflorescence 5-10 cm long, elongating at fruit maturity to 10-20 cm. Floral bracts 2-3 cm long, yellow-green on the basal 2/3, distally yellow varying uncommonly to orangish yellow or rarely to red, 8-12 mm wide, ovate to broadly oblanceolate obovate, entire or with a pair



Map 1. Distribution of *Castilleja purpurea*, *C. genevievana*, and *C. integra* in Texas.



Map 2. Detailed distribution of *Castilleja genevievana* and *C. integra* in Texas. Two collections of *C. integra* from Deaf Smith County are not shown.

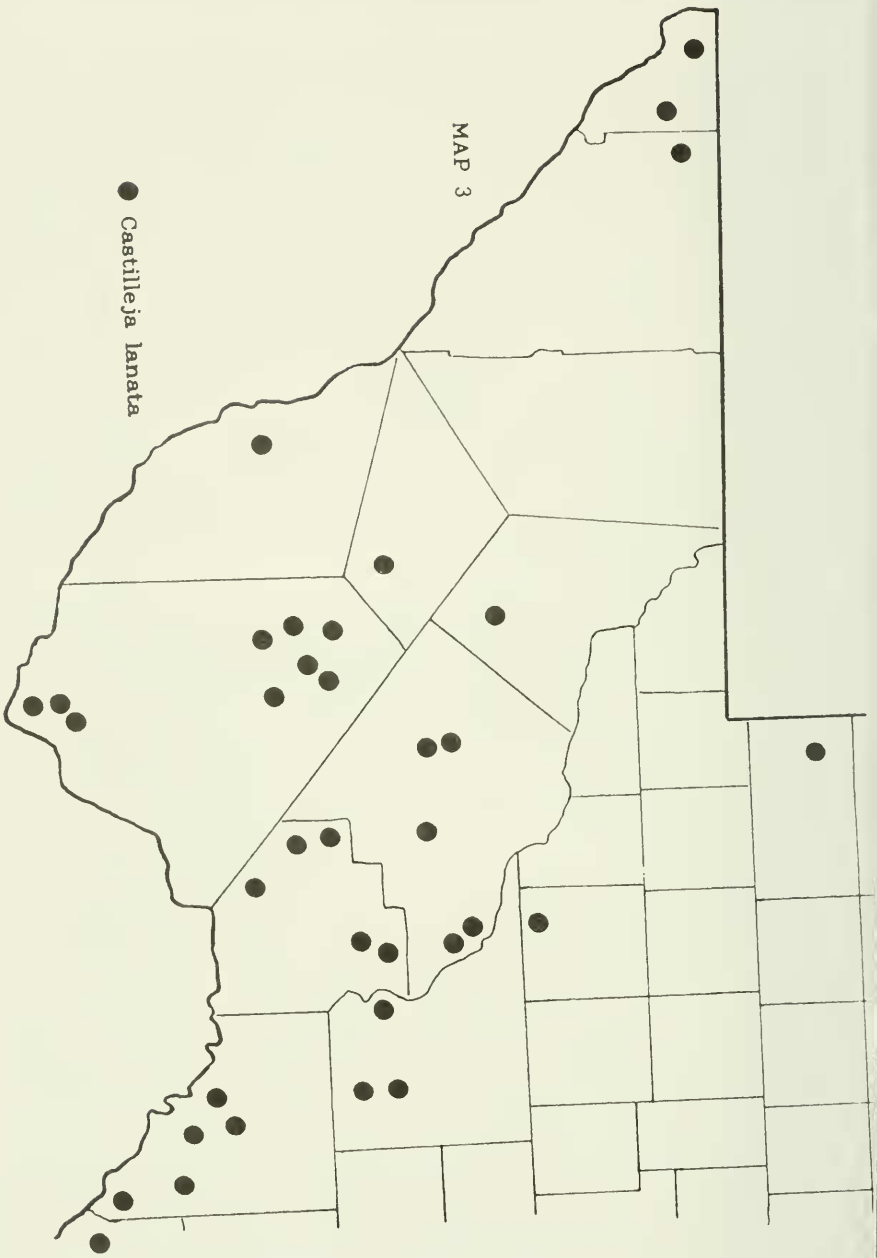
of narrowly lanceolate lobes originating slightly above the middle, the upper bracts densely stipitate glandular, without other hairs. Calyces 23-27 mm long, yellow to orangish yellow at least distally, the primary lobes 10-15 mm long, the secondary lobes 4-7 mm long, the primary lobes 1.7-2.5 times longer, densely stipitate glandular distally, without other hairs. Corollas 24-31 mm long, the 3 teeth of the lower lip 2-4 mm long, usually distinctly thickened, distally yellow, the tube light yellow, the galea 7-12 mm long, 1/3-2/5 the corolla length, with yellow to white or pink margins, the dorsal surface green to yellowish, densely short glandular; stigma and style exserted 1-4 mm, the stigma weakly to strongly recurved at maturity, with ovate branches. Mature fruits ovate, 10-15 mm long, 6-8 mm wide. Color photograph in Warnock (1970, p. 125, no. 4), as "*C. citrina.*"

Rocky, limestone hills of southcentral Texas and adjacent Coahuila, México, vegetation dominated by juniper, 1700-2800 ft; midMarch through midJune.

Additional specimens examined: MEXICO. Coahuila: Mpio. Villa Acuña, open country between Rancho Santo Domingo and Hacienda Piedra Blanca, 4 Jul 1936, *Wynd & Mueller 487* (GH).

UNITED STATES. Texas: Crockett Co.: 23 mi W of Ozona, 30 Apr 1970, *Correll & Correll 38524* (LL); Salviastrum Mesa, 32 airline mi NW of Ozona, frequent on talus slope, 23 Apr 1947, *Cory 53424* (SMU); 25 mi W of Ozona, 7 May 1947, *McVaugh 8208* (SMU,TEX-2 sheets); Read Ranch, 14 mi SE of Ozona, 3 Jul 1961, *Read A-18* (SRSC); 7 mi S of Ozona on Hwy 163, 1 Jun 1963, *Read 141* (SRSC); 15 mi E of Pecos River on Hwy 290, top of Batchlor Hill, 15 Apr 1964, *Read 593, 594*, and *595* (SRSC); 20 mi W of Ozona, 14 Apr 1949, *Tharp & Havard 49358* (TEX); 14.8 mi W of Ozona, 2400 ft, 14 Mar 1949, *Turner & Warnock 274* (LL,SMU,SRSC); 14 mi N of Juno in limestone soil, 2000 ft, 1 May 1949, *Warnock & Turner 765* (SMU,SRSC); 5 mi E of Pecos River on Hwy 290, limestone bluff above Live Oak Creek, 11 May 1947, *Whitehouse 18689* (SMU). Pecos Co.: Sheffield, 20 Apr 1931, *Jones 18287* (MO); 14 mi N of Sheffield, 1 Jun 1957, *Warnock 14907* (LL,SRSC). Upton Co., no other locality data, 7 May 1938, *Cory s.n.* (TEX). Val Verde Co.: limestone bluffs above Pecos River, 26 mi N of Langtry, 30 Mar 1947, *Warnock 47-279* (SRSC-2 sheets); 2 mi N of Devil's River crossing along Hwy 163, 1 May 1949, *Warnock & Turner 759* (SRSC); 22 mi N of Comstock on Hwy 163, 1 May 1949, *Warnock & Turner 765* (SRSC).

The new species is named for my yellow haired daughter, an avid outdoorsman and happy participant in the collection of the type. *Castilleja genevievana* is restricted to the southwestern corner of the Edward's Plateau (Maps 1 and 2). At the western margin of its range, there is a corresponding, abrupt vegetational discontinuity at the edge of the juniper dominated landscape moving westward into areas of *Larrea*. The geographic position of *C. genevievana* intermediate between its two close relatives is matched by its habitats at an intermediate range of elevation (1700-2800 feet). *Castilleja integra* occurs at



Map 3. Distribution of *Castilleja lanata* in Texas.

elevations of (2800-)3200-8600 feet in Texas; *C. purpurea* ranges over a number of different vegetational zones in Texas but occurs at 300-1750 feet in elevation, with rare outlyers (var. *citrina* in Ector and Schleicher Cos.) up to 2500 feet.

Castilleja genevievana, *C. purpurea*, and *C. integra* are similar in their perennial duration, lightly lanate stem vestiture, 3 veined leaves with distinctly reduced adaxial vestiture, and the dimensions and morphology of their bracts and flowers. Further, the stem and leaf hairs of all three have a strong tendency to be retrorsely oriented. *Castilleja genevievana* differs from *C. integra* in the yellow (vs. red) pigmentation of its floral bracts and calyces and in its vestiture of unbranched hairs (see discussion below, following *C. elongata*). In contrast, *C. genevievana* is similar to *C. purpurea* var. *citrina* in its pigmentation and unbranched hairs, as well as the narrowly lanceolate bracteal lobes. It differs from *C. purpurea* in its entire leaves, although rare plants of *C. genevievana* may produce lobed leaves on the upper half of the stems.

The floral bracts of most plants of *Castilleja genevievana* are distally yellow; they vary to orangish yellow or rarely slightly orangish (label data of *McVaugh 8208*) or rarely vary within populations from "yellow, orange, to scarlet" (label data of *Warnock 47-279*) or from yellow ("common," *Read 593*) to yellowish orange to reddish ("rare," *Read 594*) or orangish ("rare," *Read 595*). Of the ca. 80 plants of the population from which the type collection was made, all except two produced bracts and calyces with a bright, lemon-yellow color. The two exceptions were distinctly orangish.

Castilleja genevievana is probably most closely related to *C. purpurea* var. *citrina*, in view of their predominately yellow pigmentation (almost certainly a specialization within this group of related taxa). *Castilleja genevievana* and var. *citrina* produce only unbranched hairs (an unspecialized condition, see discussion below) and never bear the distinctive branched hairs characteristic of *C. integra* and *C. lanata* A. Gray. The new species might have been reasonably included as a fourth variety of *C. purpurea*, closely related to var. *citrina*, but the other three recognized varieties differ from *C. genevievana* in their consistent production of lobed leaves (1-2[-3] pairs of lobes) from the bottom to top of the stems (vs. leaves entire in *C. genevievana*) and corollas with the lower lip of three thin and at least distally petaloid, ovate lobes 4-7 mm long (vs. thickened, lanceolate, and 2-4 mm in *C. genevievana*). Further observations on variation within *C. purpurea* are given below.

According to Holmgren (1971, p. 26), "Most of the closely related species in *Castilleja* probably could not stand the test of sympatric maintenance." The same may be true for *C. integra*, *C. purpurea*, and *C. genevievana*, because they are geographically separated. Each, however, is immediately distinguishable by morphological features, and all three can justifiably be recognized at an equivalent taxonomic rank.

II. Variation in *Castilleja purpurea* in Texas

The geographic range of *Castilleja purpurea* extends from central Texas (Map 1) through Oklahoma to southern Kansas. Yellow bracted plants (var. *citrina*) occur from Texas to the northern extremity of the range of the species; purple bracted ones (var. *purpurea*) are found from southern Oklahoma to northcentral Texas; red to orange bracted ones (var. *lindheimeri* [A. Gray] Shinners) are endemic to southcentral Texas.

Plants within single populations of var. *purpurea* are strikingly variable in coloration: the bracts and calyces are predominately pinkish purple but vary from red, to reddish orange, burnt orange, peach, light yellow, creamy (very light orange-yellow), and rarely white. Similar variation has been noted on the labels of collections from Eastland Co. (*McVaugh 8338*-TEX), Hamilton Co. (*Correll & Johnston 21098*-LL), Hill Co. (*Lundell 11309, 11310, 11311, 11312, 11313, 11314*-all LL), McLennan Co. (*Nesom 7276*-TEX), and other localities. In addition, a great deal of infrapopulation variation occurs in bract and flower size: the bracts 20-40 mm long, the corollas 25-40 mm long. Similar variation in size also occurs in the other varieties of *Castilleja purpurea*.

Plants of var. *lindheimeri* produce predominately reddish orange to orange bracts and calyces, but a red color is commonly produced similar to that of typical *Castilleja integra*. A citrinalike yellow occurs rarely: in one population (Comal Co., *Nesom 7284*-TEX), one plant with three branches of orange flowers also produced a single branch with yellow flowers; in another (Travis Co., *Nesom 7275*-TEX), two yellow-bracted plants occurred in a predominately red bracted population, and several individuals were intermediate. I have tentatively treated these as populational variants of var. *lindheimeri*. The typical coloration of var. *lindheimeri* might be regarded as only a small subset of that occurring in var. *purpurea* (except for the citrina yellow, which does not appear as normal variation within var. *purpurea*), but there appears to be a relatively abrupt geographic transition between the two (Map 1), and they can be justifiably maintained as weakly delimited varieties.

Populations of var. *citrina* are considerably less variable in coloration than in the other two varieties of *Castilleja purpurea*. The bracts and calyces are tipped with bright lemon-yellow, uncommonly with yellowish orange. In the southern portion of the range of the species, var. *citrina* and var. *lindheimeri* apparently are essentially allopatric or nearly so (Map 1); the ranges of var. *citrina* and var. *purpurea*, however, more closely approach each other. In McCulloch and Menard cos., near the juncture of the two taxa, populations of var. *purpurea* are even more variable than normal and include plants with yellow bracts and calyces that do not appear elsewhere in its range. One such population (3 mi N of Brady, McCulloch Co., *Nesom 7282*-TEX) produced an astounding array of individuals with red, pink, purple, orange, yellow, and white bracts and calyces. Along Highway 190 for about 25 miles, from

near Brady (McCulloch Co.) towards Menard (Menard Co.), populations of normally variable var. *purpurea* alternate with presumably hybrid populations producing yellow variants. Westward from about six miles east of Menard, all plants are yellow bracted var. *citrina*, without any evidence of introgression from var. *purpurea*.

Genes of var. *citrina* apparently are present in populations of var. *purpurea* in their region of contact, but not vice versa, as if var. *citrina* were serving only as the pollen parent of the putative hybrids. Chromosome counts and field observations at additional localities will be necessary in a more critical assessment of the relationship between all three varieties of *Castilleja purpurea*.

Castilleja purpurea (var. *purpurea* and var. *lindheimeri*) commonly grows with *C. indivisa* Engelm. along the eastern margin of the Edward's Plateau. The latter is native to eastern Texas, southeastern Oklahoma, and western Louisiana but is now also widely seeded by the Texas Highway Department for its beauty along roadsides. *Castilleja indivisa* is closely related to the widespread Mexican species *C. scorzoneraefolia* Kunth and relatives (see Nesom 1992), including the Texas species *C. rigida* Eastwood (see below), but where *C. indivisa* grows with *C. purpurea*, hybrids between the two species are common. At one such roadside locality in Coryell County (*Nesom 7279/7280*-TEX), intermediates and apparent backcrosses toward both parents produced a wide range of combinations of morphological features, including bract and calyx color, corolla, calyx, and leaf morphology, duration (judging from the root development), and habit. At several localities in Hays County (e.g., *Nesom 7283*-TEX), where *C. indivisa* was not artificially seeded, hybrids between it and *C. purpurea* were relatively common, and no individuals of the former without genetic influence of the latter could be found.

III. Two putatively rare and endemic taxa of trans-Pecos Texas

The status of *Castilleja elongata* Pennell

In his study of the Scrophulariaceae of trans-Pecos Texas, Pennell (1940) described *Castilleja elongata*, which he considered to be a narrowly endemic species. It has generally been acknowledged to occur on Emory Peak of the Chisos Mountains in Brewster Co., although specimens from the Davis Mountains of Jeff Davis Co. have also been identified as *C. elongata*.

The original description of *Castilleja elongata* was based only on the type specimen, and Pennell's sole comment regarding it (1940, p. 307) was that it "would seem to be the representative of the group of *Castilleja miniata* Dougl. [*ex* Hook.] in the mountains of the Big Bend district of southern Trans-Pecos Texas." In contrast, with many collections now available for study from trans-Pecos Texas, I can find no feature to separate *C. elongata* from the widespread

and variable *C. integra*. Holmgren (1970) distinguished *C. elongata* from *C. integra* by its stems "finely villose" (vs. "whitish-tomentose or lanate") and its bracts "not glandular-pubescent" (vs. "glandular-puberulent on the colored portions"). All *C. integra*-like plants of Brewster Co., however, produce bracts that are prominently glandular on the distal portion with short, capitate hairs, these usually mixed with nonglandular hairs, and the stems of such plants are highly variable in the amount of vestiture produced. In the present study, I have examined 58 collections (not including duplicates) of *C. integra* from Brewster Co.; fifteen of these are from the Chisos Mountains.

Castilleja integra in Brewster Co. occurs at 3600-6200 feet, outside of the Chisos Mountains, where it occurs at 5500-7500 feet; elsewhere in Texas it has been collected at elevations of 5000-7500(-8600) feet in Jeff Davis Co., 4150-7500(-8000) feet in Culberson Co., and 5900-7000 feet in El Paso Co. At the higher elevations, plants tend to be more variable in height, ranging somewhat taller (to 1 meter or more in the Chisos Mountains), with a somewhat reduced amount of vestiture, and they produce calyces and corollas that range to near the low end of the range of length for the species. Within these atypical populations, however, the intergradation in stature, vestiture, and floral size with plants of lower elevations appears to be complete.

The same phenomena were observed in *Castilleja integra* in New Mexico by Standley (1909, p. 86), who noted that in the Organ Mountains, "it grows at an altitude of about 6000 feet, on shaded slopes, where it is a tall plant and but little branched. Farther north, in the region about Santa Fe it is very low and much branched, growing on the open mesas and foothills, but at about the same altitude. The size of the flowers and bracts varies noticeably in different plants ... Most of these variations, perhaps, are due to climatic conditions, especially temperature and the water content of the soil."

Castilleja integra occurs from Arizona to Colorado, New Mexico, and Texas and in the Mexican states of Durango, Sonora, Chihuahua, Coahuila, and Nuevo León. Over almost its entire geographic range, it produces red to scarlet floral bracts, calyces, and corolla margins. There are three named varieties of the species, all red bracted, at the northern and northwestern edges of its range: from Arizona, var. *gloriosa* (Britt.) Cockerell (The Southwest 2:134. 1900.); from Colorado, var. *gracilis* Cockerell (Bull. Torr. Bot. Club 17:35. 1890.); and from New Mexico, var. *intermedia* Cockerell (The Southwest 2:134. 1900.). The taxonomic status of these is not evaluated here, but only the first has generally been recognized in regional floristic treatments. I have, however, examined specimens from over the entire range of *C. integra*.

Warnock (1977, p. 201) noted that "color variation is unusual" in *Castilleja integra* and provided a photograph of a rare variant with yellow bracts from a primarily red bracted population about 10 miles south of Alpine in Brewster Co. I have observed only three collections of such a yellow variant of *C. integra*: (1) *Scott 2* (SRSC) from near Panther Junction in Brewster Co. - *Scott 1*

(SRSC) from the same area is typical red bracted *C. integra*, (2) *Steiger 1212* (NY) from Boot Canyon in the Chisos Mts., and (3) *Stewart 1739* (GH) from the Sierra de la Encantada in northwestern Coahuila, México. The occurrence of these yellow bracted but otherwise typical plants of *C. integra* along the very eastern margin of the species range, facing the geographic ranges of two, yellow bracted, closely related taxa (*C. genevievana* and *C. purpurea* var. *citrina*), seems likely to be indicative of an earlier genetic connection between all three.

Among all of these populations of *Castilleja integra*, one feature in particular appears to indicate their genetic coherence. While most of the hairs of the stems and leaves are unbranched, at least some of them are branched. The basal cell varies in length from ca. 0.02-0.10(-0.40) mm, then branches into two thinner, divergent cells that are also variably elongated and contribute to the lanate appearance of the vestiture. I have not been able to discover a geographic pattern that would predict the relative abundance (branched/unbranched) of the branched hairs, which varies from about 0.1-10.0 percent (or sometimes greater on the leaves). All plants over the entire range of the species produce branched hairs at least at a low frequency.

In trans-Pecos Texas, *Castilleja lanata* is the only other species with branched hairs similar to those of *C. integra*. The former is easily identifiable by the dense, close, white woolly pubescence of its stems and both surfaces of its leaves. All of the hairs are composed of a short stipe with 2-4, elongated lateral branches (up to 2 mm long) produced at the apex of the stipe and that form the mass of the conspicuous vestiture.

Few other American species of *Castilleja* are known to produce branched hairs, among them *C. dendridion* Nesom and *C. galehintoniae* Nesom from México (see Nesom 1992) and *C. pruinosa* Fern. and individuals of *C. applegatei* Fern. var. *fragilis* (Zeile) N. Holmg. of the northwestern United States. Except for *C. dendridion*, the hairs of these taxa are similar to those of *C. integra* and *C. lanata*, but they tend to produce secondary branches. Holmgren (1971) considered the similarity in trichome morphology significant enough to support an hypothesis of introgression between the two northwestern U.S. taxa, which otherwise are relatively distantly related between themselves. It also seems plausible that the branched hairs of *C. integra* indicate a close relationship between it and *C. lanata*. Complicating this hypothesis somewhat is the observation that the rare endemic, *C. organorum* Standley of the Organ Mountains in southeastern New Mexico, also bears a low percentage of branched hairs similar in morphology to those of *C. integra* and *C. lanata*, both of which also occur in the Organ Mountains. The calyx of *C. organorum*, however, is asymmetrically divided, and its evolutionary relationships are probably more closely linked to *C. wootonii* Standley and *C. linariifolia* Benth. (see comments below).

Castilleja lanata and *C. integra* are sympatric over the greatest parts of their geographic ranges. The former has a slightly broader range than the lat-

ter, occurring at lower elevations and further to the south in México. *Castilleja integra* occurs at higher elevations and slightly further to the north (northern New Mexico and southern Colorado), and even in the area where *C. lanata* does not occur, the vestiture of *C. integra* includes branched hairs at least at a low frequency. This may indicate that branched hairs were present in the ancestral populations of *C. integra*, rather than acquired through later hybridization and introgression with *C. lanata*, although the latter processes might account for the variation in abundance of branched hairs in *C. integra*. *Castilleja integra*, however, is more similar to *C. genevievana* and presumably shares with it a more recent common ancestor. *Castilleja lanata* is partially sympatric with *C. genevievana* (Maps 1 and 3) with no evidence of gene flow.

Chromosome numbers have been reported from numerous populations of *Castilleja integra* (Heckard 1958, 1968; Heckard & Chuang 1977; and Ward 1983, 1984). In each of Arizona, Colorado, and New Mexico, both diploids (n=12) and tetraploids (n=24) are known, and Heckard & Chuang (1977, p. 163) noted that "No cytogeographic pattern is apparent in the distribution of the two chromosome levels in this fairly wide-ranging species." Lockwood & Forstner (1991) reported a hexaploid of *C. integra* from near Alpine and a diploid of *C. elongata* from the Chisos Mountains (both from Brewster Co., Texas). Unpublished chromosome counts (as specimen annotations in 1991 by Lockwood at SRSC) indicate that tetraploid populations of *C. integra* also occur in trans-Pecos Texas. The single reported chromosome count of *C. lanata* (Ward 1983) has been diploid.

My interest in the systematics of Texas *Castilleja* was begun without knowledge of another very recent study that included some of the same plants reported on here. I studied the SRSC collections annotated by Mark Lockwood but did not examine his thesis (1991) until after the essential completion of my own manuscript. The strong contrasts in our approaches and conclusions, discussed below, are the result of totally independent studies.

A strong point of disagreement between the present study and Lockwood's (1991) concerns the nature of variability within what can be accepted as *Castilleja integra*. According to Lockwood (p. 86), "The seed-coat similarities between *C. elongata* and [plants from Mt. Livermore in the Davis Mountains identified by the yet unpublished epithet "livermorensis"] also suggest that these two species are very closely related, at least phenetically. This allows for the possibility that they may also represent relictual populations of a once widespread species that has undergone speciation in the isolated montane habitats of the Davis and Chisos Mountains. *Castilleja integra* is also closely related to these two species and possibly shares a common ancestor; ...." In contrast, I suggest that *C. integra* itself is the "once [and still] widespread species" postulated by Lockwood and that some of its relatively high elevation populations are slightly divergent from the morphological form more typical for the species at lower elevations.

Lockwood's key to *Castilleja integra*, *C. elongata*, and "livermorensis" uses only aspects of vestiture and floral bract morphology that I find to be quantitative and intergrading, as discussed above. His data show the calyces and corollas of *C. integra* to be longer than in the other two taxa, where only slight differences in size are shown. In contrast, I did not observe any discontinuous differences in size within what is here recognized as *C. integra* in Texas.

With a more detailed knowledge of the cytogeographical variation, the high elevation forms of *Castilleja integra* in southwestern Texas might indeed prove to be relictual diploids, with intervening areas of the species range primarily filled by polyploids. Diploids of *C. integra*, however, are known to be scattered through a large part of the range outside of Texas. Further, regional differentiation apparently occurs quickly in the genus, as evidenced by numerous narrow endemics and many variable species. Given the wide range of elevations, habitats, and substrates known for *C. integra*, the chromosomal variation, the intergrading morphological variability, some of it possibly reflecting genetic influence of other species, and the proposed but unevaluated varietal taxa already existing within *C. integra*, I can find no satisfactory or appropriate way to recognize segregate taxa, even at the varietal rank, within it from Texas. My view of the taxonomy of this species as it occurs in Texas is summarized below.

Castilleja integra A. Gray *in* Emory, *Rep. U.S. & Mex. Boundary Surv.* 2(1):119. 1858. SYNTYPES: UNITED STATES. Gray cited collections by Wright, Bigelow, Kreuzfeldt, Fendler, and E.K. Smith. The details of the necessary lectotypification will be discussed in a separate paper (Boufford & Nesom in prep.).

Castilleja elongata Pennell, Proc. Acad. Nat. Sci. Philad. 92:306. 1940. TYPE: UNITED STATES. Texas: Brewster Co., wooded slopes of northern Chisos Mountains, ca. 6000 ft, Aug 1934, *T.L. Steiger 1689* (HOLOTYPE: NY!).

Plants perennial. Stems 15-45(-60)(-90 in Brewster Co.) cm tall, lanose to villous, with a mixture of simple and branched hairs, the stipes 0.02-0.08(-0.4) mm long, bearing 2(-4) branches, the simple hairs and branches 0.1-0.5(-0.8) mm long. Leaves 2-6(-8) cm long, linear to narrowly lanceolate, (1-)2-7(-9) cm long, (1-)2-6(-8) mm wide, the lower surfaces densely invested but not obscured by stiff, short, somewhat retrorsely oriented hairs, the longer of these also commonly apically branched. Bracts entire or with 2 lobes originating from middle to near the apex, the apices with capitate glandular hairs. Calyces (18-)21-35(-38) mm long, the primary lobes (7-)10-16(-18) mm long. Corollas (23-)28-42(-47) mm long, the galea (8-)10-17 mm long, the tube 17-27(-30) mm long.

Limestone and igneous substrates; (2800-)3200-8000(-8600) ft; flowering late Mar-Sep(-Oct).

The status of *Castilleja ciliata* Pennell

A population of plants thought to be endemic to the Davis Mountains of Jeff Davis Co., Texas, has been recognized and maintained as *Castilleja ciliata* (Holmgren 1970). Comparative study of these, however, shows them to be conspecific with plants of the Sacramento and White Mountains of southeastern New Mexico, where they are known by the earlier name *C. wootonii*. These are tall perennials with glabrous or very sparsely hairy stems, except in the inflorescence and lowermost portions, which commonly are villous. The linear leaves also range from very sparsely pubescent to completely glabrous or with only short ciliate margins. Those from New Mexico tend to be slightly hairier than the Texas plants, but all are unquestionably the same species. No collections of *C. wootonii* are known from the Guadalupe Mountains, which are in a nearly intermediate geographic position between the Davis and Sacramento Mountains.

The only apparent influence from other species on any of the plants of *Castilleja wootonii* examined in this study is observed in Worthington's collection *12134* (UTEP) from Otero Co., New Mexico. One of the three mounted stems is typical *C. wootonii*; the other two, while nearly identical to the first in overall morphology, have stems sparsely invested with unbranched, retrorsely appressed hairs. The source of this variation is equivocal, but the plants may be hybrids with *C. integra*, which is common in the same area.

Pennell (1940) compared *Castilleja ciliata* to *C. miniata*, but the latter differs in its nearly equally divided calyx (vs. unequally divided in *C. wootonii*). The key provided by Wooton & Standley (1915) contrasted *C. wootonii* with *C. linariifolia*, the latter a widespread species of the western United States and according to Holmgren (1976) a member of subg. *Castilleja*, although it sometimes hybridizes with the relatively more dissimilar *C. miniata* (see notes by Holmgren [1984]). Plants of both *C. linariifolia* and *C. wootonii* produce glabrous or nearly glabrous stems, thick, linear-lanceolate leaves, and unequally divided calyces. Although the former tends to produce more strongly unequal calyx lobes, it is clearly closely related, if not conspecific, with *C. wootonii*. The couplet in Wooton & Standley's treatment compared these two taxa in features of their leaf morphology, but with many specimens of each taxon now at hand, the putative foliar differences appear to be completely overlapping. The following couplet provides an updated comparison of the two taxa.

1. Calyx clefts 10-20(-22) mm deep abaxially and 2-6(-12) mm adaxially, the abaxial clefts 3-5 times longer than the adaxial; bract margins short hispid; lower portion of the stems glabrous to villous. ... *C. linariifolia*

1. Calyx clefts 11-14 mm deep abaxially and 8-9 mm adaxially, the abaxial clefts 1.2-1.8 times longer than the adaxial; bract margins densely long-ciliate; lower portion of the stems villous. ..... *C. wootonii*

Castilleja wootonii Standley, Muhlenb. 5:84. 1909. TYPE: UNITED STATES. New Mexico: [Lincoln Co.,] White Mountains, 7400 ft, 25 Aug 1907, *E.O. Wooton & P.C. Standley 3411* (HOLOTYPE: NY! *ex* NMC, NMC-photo!). In the protologue is additional and conflicting collection data ("Gilmore's ranch on Eagle Creek," at "about 3400 feet"), but it seems reasonable that the NY specimen represents authentic type material.

Castilleja ciliata Pennell, Proc. Acad. Nat. Sci. Philad. 92:306. 1940. TYPE: UNITED STATES. Texas: Jeff Davis Co., Davis Mountains, rocky slopes of Mt. Livermore, 2200 m, 6 Jun 1928, *E.J. Palmer 34383* (HOLOTYPE: PH!; Isotype: NY!). The PH specimen was annotated in an undated, unsigned note as "=*C. wootoni* Standl. *fide* Pennell."

Additional specimens examined: UNITED STATES. New Mexico: Lincoln Co.: White Mts.: Eagle Creek Canyon, ca. 7 mi NW of Ruidoso, locally common on shady aspects of S-facing exposed granite faces, pine-oak-Douglas fir, 11 Jul 1982, *Soreng, Spellenberg, & Ward 2024*, voucher for chromosome count of n=12, reported by Ward 1983 (NMC); N of Sierra Blanca on trail to MonJeau lookout, 8 Sep 1970, *Spellenberg 2392* (NY); White Mt. Peak, 1897, *Wooton s.n.* (NMC) and 1901, *Wooton s.n.* (NMC); ca. 2.0 mi W of Sierra Blanca Ski Lodge, lower part of Apache Bowl Ski Area, open meadows, 11,000 ft, 28 Jun 1980, *Worthington 6148* and *6149* (UTEP); ca. 1.0 air mi W of the Sierra Blanca Ski Resort, bottom of ravine through conifer forest near stream, 10,800 ft, 5 Jul 1981, *Worthington 7227* (UTEP); entrance to Sierra Blanca Ski Area, ca. 9800 ft, 7 Aug 1984, *Worthington 12307* (UTEP). Otero Co.: White Mts.: [no other data], Jun 1936, *Hinckley 1024* (NY,TEX); divide above the Mescalero agency, 1895, *Wooton s.n.* (NMC); Sacramento Mts.: Cloudcroft pine-spruce-aspen, partly open, wooded slopes, 19 Aug 1968, *Correll & Correll 36130* (LL); Mescalero Apache Indian Reservation, Silver Lake, 2450 m, 3 Jul 1979, *Freeman s.n.* (UTEP); S of Cloudcroft, 21.1 mi along State Rd. 24, Cathey Canyon Vista, open grassy area in dry pine forest, 6 Jul 1983, *Hardison 11* (TEX); Cloudcroft, Fir Campground, rocky hillside with pine and fir, 17 Jul 1965, *Iwen 199* (TEX); Sacramento's Silver Campground, 8 Sep 1979, *Patrick s.n.* (UTEP); High Rolls, 19 Oct 1969, *Smartt 43* (UTEP); Cloudcroft, 19 Oct 1969, *Smartt 93* (UTEP); vicinity of Toboggan (an old settlement) ca. 3.5 mi W of Cloudcroft in bottom of canyon, pine-oak-Douglas fir, 10 Aug 1969, *Spellenberg 2081* (NMC); Cloudcroft, 1899, *Wooton s.n.* (NMC); Mescalero reservation, 1905, *Wooton s.n.* (NMC); canyon between entrance to Sunspot and road S down Sacramento Canyon, N slope, limestone

soil, edge of Douglas Fir, 9100 ft. 28 Jul 1979, *Worthington 4793* (UTEP); Bailey Canyon ca. 2 mi NW of Cloudcroft, mixed pine-fir forest, 8400 ft, 1 Aug 1982, *Worthington 8572* (UTEP); upper Russia Canyon ca. 0.2 mi E of Hwy 64, 8900 ft, 24 Jun 1984, *Worthington 12134* (UTEP). Texas: Jeff Davis Co., Davis Mts.: common on Livermore peak and spur ridges, 9-12 Jul 1921, *Ferris & Duncan 2552* (NY); Oct 1937, *Hinckley "985"* (TEX); infrequent in moist canyons at higher elevations, high gorge of Madera Canyon on W slope of Mount Livermore, ca. 2350 m, 26 Jul 1937, *Hinckley 985* (NY-2 sheets); Mt. Livermore, W branch Madera, oak woodland, ca. 2300 m, 27 Aug 1939, *Hinckley s.n.* (GH); Tobe gap, 1/4 mi W of Mt. Livermore peak, 30 Sep 1991, *Lockwood 288* (SRSC); N slope of Mt. Livermore near peak, 30 Sep 1991, *Lockwood 296* (SRSC); Turman Ranch ca. 4 mi SSE of Mt. Livermore at upper end of Merril Canyon, steep N-facing slope in very rocky soil, beneath *Pinus cembroides* and *Quercus gambellii*, 20 Oct 1990, *Lockwood 193* (SRSC); N slope of Mt. Livermore on steep grassy slope in open area, 16 Oct 1990, *Lockwood 188*, voucher for chromosome count of n=12, reported by Lockwood & Forstner 1991 (SRSC); infrequent at upper spring in Madera Canyon, 11 Sep 1947, *Warnock 7460* (SRSC,TEX); 0.8 air mi SE of top of Mt. Livermore, just over N side of crest of mountain, semi-open grassy area, 7800-7900 ft, 2 Sep 1979, *Worthington 5155* (SRSC,TEX,UTEP); 18 Aug 1914, *Young s.n.* (TEX); 16 Sep 1918, *Young s.n.* (TEX).

Pennell's hypothesis that *Castilleja ciliata* is most closely related to *C. miniata* was adopted by Lockwood (1991). Lockwood's claim (p. 70) that his data "show unequivocably that Pennell was correct ..." in this view and his suggestion (p. 86) that "perhaps *C. ciliata* was derived from a relictual population of *C. miniata* ..." are unjustified, because the only taxa of *Castilleja* included in his study were *C. ciliata, C. miniata*, and *C. integra* (including the two trans-Pecos segregates). For the same reason, there is no support for Lockwood's assertion (p. 89) that the flavonoid components of these five taxa show them to be "unequivocally ... closely related, perhaps even at the sectional or other infrageneric level, within the genus." His study of flavonoids, seed coat morphology, and pollen morphology provide positive evidence for placing the plants involved into two groups, *C. ciliata* and *C. miniata* vs. the *C. integra* complex, but no evidence for any other taxonomic conclusions. I have not seen a specimen representing what Lockwood referred to (p. 70) as "possibly a relictual population of *C. miniata*" from Mount Livermore.

IV. The identity of *Castilleja latebracteata* Pennell

Castilleja rigida is the correct name for the plants of trans-Pecos Texas that have been identified as *C. latebracteata* (Holmgren 1970), and most recently as *C. nervata* Eastwood (Johnston 1990; Hatch *et al.* 1990). It is a relatively

common species of the Chihuahuan Desert region in the Mexican states of Durango, Zacatecas, Chihuahua, Coahuila, and Nuevo León (see Nesom 1992 for details). Map 4 shows the distribution of *C. rigida* in Texas, where it is not known to hybridize with any other species.

V. The identity of *Castilleja tortifolia* Pennell

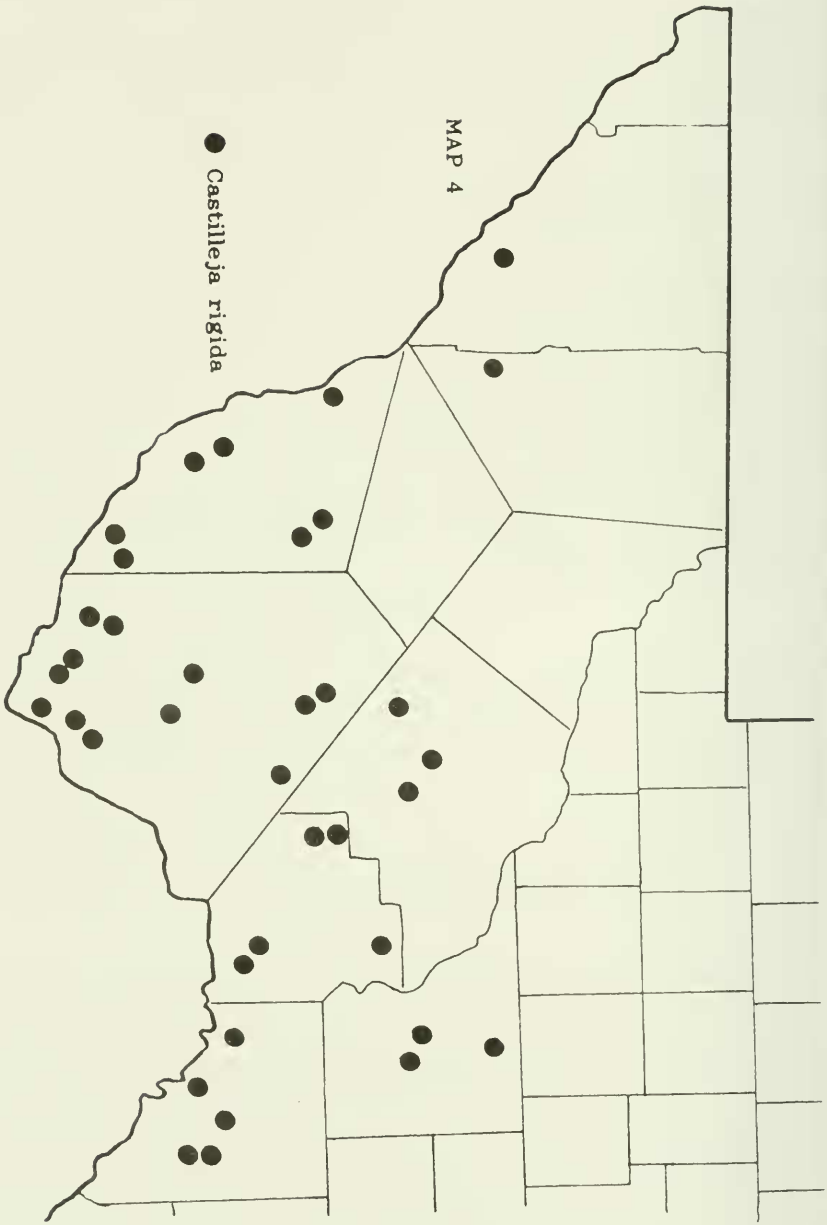
In his discussion following the description of *Castilleja tortifolia*, Pennell noted that it is closely related to *C. mexicana* (Hemsl.) A. Gray, differing in aspects of its leaf morphology and its white (vs. yellow) flowers. With many more specimens now available for study, however, it is clear that only a single species is represented. This was also tentatively surmised by Holmgren (1970) and confirmed by him in 1980, as evidenced by his identification and annotations of specimens in LL,TEX. *Castilleja mexicana* is represented in collections I have studied from the Mexican states of Durango, Chihuahua, Zacatecas, Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, and Aguascalientes and from trans-Pecos Texas (Map 5) in Brewster, Culberson, Jeff Davis, and Presidio counties.

Castilleja mexicana (Hemsl.) A. Gray. BASIONYM: *Orthocarpus mexicana* Hemsl., *Biol. Centr.-Amer. Bot.* 2:463, t. 63. 1882. TYPE: MEXICO. Zacatecas: *Coulter s.n.* (HOLOTYPE: K, not seen). *Castilleja mexicana* (Hemsl.) A. Gray, Proc. Amer. Acad. Arts 21:404. 1886.

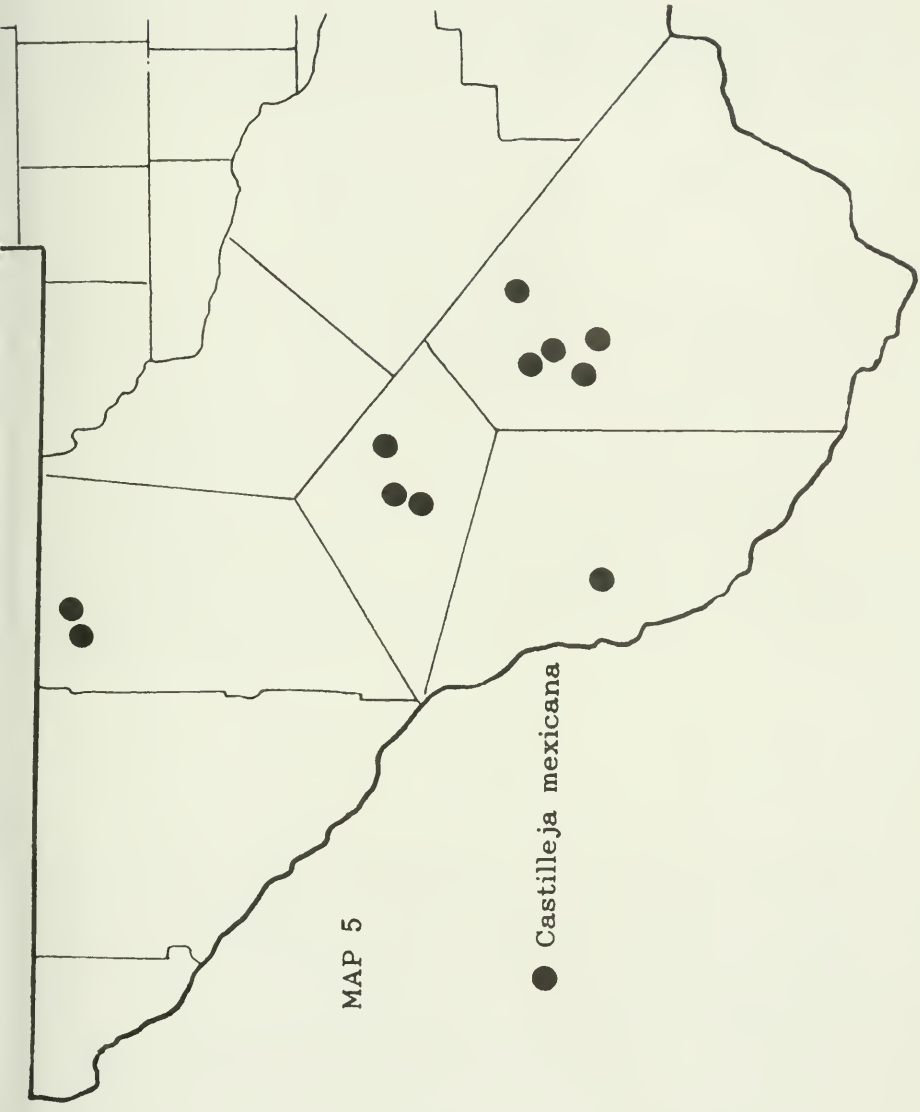
Castilleja tortifolia Pennell, Proc. Acad. Nat. Sci. Philad. 92:304. 1940. TYPE: UNITED STATES. Texas: Jeff Davis Co., Davis Mts., rocky open ground near Livermore Peak, 2500 m, 14 Jun 1926, *E.J. Palmer 30867* (HOLOTYPE: PH!).

Castilleja mexicana is sometimes confused with *C. sessiliflora* Pursh, the latter of which is by far the more abundant and widespread species in Texas (Map 6) and which occurs from southeastern Canada southward primarily through the Great Plains to Illinois and Missouri, Colorado, Arizona, and Texas, and the Mexican states of Coahuila and Nuevo León. Both species are distinctive in their falcate corollas long exserted from the calyx, but they can be easily distinguished by reference to the following comparison.

1. Plants annual or short lived perennials from a woody but slender taproot; bracts yellow; stems with a mixture of stiffly spreading nonglandular and gland tipped hairs; primarily igneous substrates, 4300-6600 ft in Texas, flowering late Mar-Jul(-Sep). ..... *C. mexicana*



Map 4. Distribution of *Castilleja rigida* in Texas.



Map 5. Distribution of *Castilleja mexicana* in Texas.

Map 6. Distribution of *Castilleja sessiliflora* in Texas.

1. Plants perennials from a woody, distinctly thickened root; bracts pink to yellow; stems nearly lanose with long, somewhat intertwined, nonglandular hairs; limestone and gypsum substrates, (950-)2100-5400 ft in Texas; flowering Mar-Jul(-Oct). ..... *C. sessiliflora*

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